

by employing a formula as provided by Article H.2 of the International Code with particular attention to the "Note."

Goodman (1950), in describing his *P. engelmannii* var. *glabra*, almost certainly had at hand a biotype of Engelmann's spruce that showed the result of the introgression of genes from the glabrous White spruce.

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FIELD STUDIES OF NATURAL HYBRIDIZATION IN THE OREGON SPECIES OF IRIS L. SUBSECTION CALIFORNICAE DIELS

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Smith and Clarkson (1956) have discussed the cytological aspects of hybridization in *Iris*, subsection *Californicae*. They reported that, with the exception of *I. tenuis* Wats., which has been removed to a new subsection (Clarkson, 1958), all the members of the subsection studied had a uniform chromosome morphology, and all contained a diploid number of forty. Fertile hybrids were produced experimentally without difficulty and all were highly fertile except that hybrids involving *I. tenuis* as a parent could not be produced. This paper will discuss some natural hybrids of those taxa occurring in western Oregon and will propose certain nomenclatural revisions. Because the subsection was treated taxonomically by Foster (1937), conventional citations will not be included except for taxa described since that time.

DISTINGUISHING CHARACTERISTICS. Aside from the usual characteristics of the genus *Iris*, the members of the subsection *Californicae* are distinguished by a usually deltoid stigma; D-shaped, cubical or ovoid seeds; the absence of foliaceous stem leaves; and tough basal leaves which are reddish at base. A number of characteristics have been used for distin-

guishing species by various authors, including Foster (1937) and Dykes (1912) in the two most complete reviews of the subsection. These have been evaluated with herbarium specimens (Clarkson, 1950) and with living material. Those characters which allow ready distinction of taxa and which are most easily utilized for study of hybrids are as follows:

Perianth. The petals are usually narrow and about the same length as the sepals which are linear to spatulate in shape. Color of the perianth ranges from white, purple, pale yellow, golden yellow, to apricot and maroon.

Perianth tube and pedicel. The perianth tube varies in length from 0.4 to 12 centimeters with the pedicel varying approximately inversely.

Bracts of the inflorescence. The bracts, or spathes, are variable in shape from ovoid to linear; in length from 2 to 15 centimeters; and in position from opposite to alternate.

FIELD STUDIES. Although a quantitative study of morphological and ecological characteristics was desirable, inadequate knowledge of distribution of the species and the absence of definite knowledge of natural hybrids made such work impossible. Field work was therefore conducted on a qualitative basis. A limited number of transplants made during current field work and previously by Smith (Smith and Clarkson, 1956) demonstrate that the characteristics of the taxa are constant under varying environmental conditions. Herbarium specimens designed to represent all the variation present in a given location were collected. These mass collections are in the possession of the author.

Results of field studies are given below together with interpretations of their significance.

HYBRIDS BETWEEN *I. TENAX* AND *I. CHRYSOPHYLLA*

Iris tenax is characterized by narrow, distant bracts; a perianth tube from 4 to 9 millimeters in length and by lavender to purple flowers with broad spatulate sepals. The plants are tall and with definite stems. Though the species is typically purple-flowered, two yellow-flowered populations have been found. One of these is along Scoggin's Creek in Washington County, Oregon. It has been treated as *I. gormanii* Piper and more recently as *I. tenax* var. *gormanii* (Piper) Foster. The second yellow-flowered population is on Monument Peak, Linn County, Oregon. This local population is apparently not well known and has not been cited in the literature of the subsection. Neither of these populations can be distinguished from the typical phase of *I. tenax* by any trait other than color.

The general range of the species is from the central part of western Washington to southern Oregon. Ecologically it is a species of unshaded conditions and is abundant on the oak-covered hills of the Willamette and Umpqua valleys. It does not extend into coniferous areas unless trees are cut, roads built, or conditions otherwise disturbed in such a way that shading is reduced. Within the general range there seem to be no soil or moisture factors limiting its distribution. Factors controlling the northern and southern limits of the species range are probably climatic in nature.

Iris chrysophylla is characterized by lanceolate, opposite bracts; a perianth tube 5 to 9 (occasionally to 12) centimeters in length; a pedicel less than 1 centimeter in length; and by pale yellow flowers with narrow perianth parts. In southwestern Oregon, where the species is most abundant, well-marked stems are produced. In the Cascade Mountains of northern Oregon, the plants are often nearly stemless. Plants at two previously unreported stations of the species, Mill Creek, Polk County, Oregon, and Prairie Mountain, Benton County, Oregon, are of the Cascade type.

Ecologically *I. chrysophylla* is a species of open coniferous forests. It grows best on drier soils and will tolerate more shade than *I. tenax*. It is a characteristic species of the ponderosa pine and ponderosa pine-Douglas fir communities of southwestern Oregon.

Distinctive hybrids between *I. tenax* and *I. chrysophylla* have been found in three locations: (1) 4½ miles up Mill Creek from the Dallas—Wallace Bridge highway, Polk County, Oregon; (2) 13¼ miles southwest of Roseburg, Douglas County, Oregon, along Oregon State highway number 42; (3) steep hills along the first tributary of the North Santiam River west of the Detroit Dam, Marion County, Oregon. In all three locations conditions have been disturbed by road construction.

At all three of these sites individuals have been found which are intermediate between the parent species and which cannot be assigned to either species. Bracts of the hybrids are opposite and are broader than is characteristic of *I. tenax* but not so broad as those of *I. chrysophylla*; flower color is maroon to grayish-lavender; and the perianth parts are slender. The plants are smaller than typical *I. tenax* but have a definite stem. Perianth tube length in the natural hybrids averages 2.2 centimeters and the pedicel averages 1.4 centimeters. Comparative measurements in the known hybrids are perianth tube 2.5 and pedicel 1.8. This indicates that the hybrids are possibly of the F₁ generation. In other characters the natural hybrids compare closely with the known hybrids.

The area of overlapping ranges is, in all three cases, small. At Mill Creek and along the North Santiam highway, a transect of less than 100 yards extends through the area occupied by both species. At the site southwest of Roseburg, a similar transect extends less than one-half mile.

Hybrids between these two species appear to be introgressive toward *I. tenax*. Individuals identifiable as *I. tenax* show definite *I. chrysophylla* characteristics for at least ten miles from the area where typical *I. chrysophylla* occurs. These individuals exhibit a change in color toward a pale purple; a reduction in size; and a tendency toward broader and less distant bracts. These modifications in *I. tenax* are what might be expected as a result of hybridization with *I. chrysophylla*. The intermediates previously discussed are found in the areas where the two species occur together but *I. chrysophylla* remains constant and no individuals of that species have been found which exhibit *I. tenax* characteristics.

Introgressive hybridization between these two species is a close parallel

of a situation described by Anderson (1949) in which hybridization is followed by backcrossing and selection of backcross types. Apparently, in this case, only the offspring of the intermediate \times *I. tenax* backcross are selected. The factors of the ecology which bring about this selection are not known. The introgression, however, has resulted in a considerable increase in the variability of *I. tenax* while *I. chrysophylla* has remained constant.

The occurrence of *I. chrysophylla* at two locations in the Coast Range of Oregon was not unexpected. The presence of individuals of *I. tenax* with lanceolate, opposite bracts in the Coast Range west of Corvallis, Oregon, suggested possible hybridization with *I. chrysophylla*. At the Mill Creek location in Polk County, Oregon, the two species are in contact at the present time, as was previously mentioned. At Prairie Mountain, Benton County, Oregon, there is no present day contact on the north and probably not on the south. *Iris chrysophylla* is abundant on a broad, well-drained meadow, along a south-facing slope near the summit of Prairie Mountain at an elevation of about 3200 feet. *Iris tenax* is not now in contact on the north, presumably because of the dense growth of Douglas fir on that side. The south side of the mountain is more open and the two species may come together though no intermediates have been found. *Iris tenax* specimens collected at Horton, Lane County, eight miles to the south, have a narrower and more pale perianth which suggests hybridization with *I. chrysophylla*.

Thirty miles north of Prairie Mountain are individuals of *I. tenax* with linear-lanceolate, opposite bracts, and narrow, pale purple perianth parts. These plants are probably the result of introgression from *I. chrysophylla* to *I. tenax*. These hybrid forms indicate either that *I. chrysophylla* is more abundant in the Coast Range than is now known or that it was more abundant in the past and has survived only on the more favorable sites. Either hypothesis may be true in part, but it seems unlikely that these forms are the result of recent hybridization. *Iris chrysophylla* has not been found in the Coast Range between Prairie Mountain and Mill Creek, and distances are probably too great for plants at those locations to be involved as parents. The most probable explanation is that *I. chrysophylla* was more abundant in the Coast Range of northern Oregon in the past and has remained only at the dry, open sites such as Mill Creek and Prairie Mountain. The occurrence of a warm, dry period in postglacial times, followed by general cooling and increase in moisture (Hansen, 1947) makes this a reasonable assumption. Whether *I. chrysophylla* was distributed throughout the general area of northwestern Oregon in the past or only on the higher peaks, is a question which cannot be answered. In either case, abundant opportunities for hybridization could have existed. Introgression, such as occurs today, could have given greater adaptive value to *I. tenax* while *I. chrysophylla* remained more nearly constant and more vulnerable to environment change.

There is, however, no reason to suppose that the yellow-flowered forms

of *I. tenax* on Monument Peak and in Washington County, Oregon, are of hybrid origin. All the hybrids between these two species, including the artificial hybrids produced for this study, exhibit a tendency toward the lanceolate, opposite bracts of *I. chrysophylla*. The purple flower color is reduced to greyish-lavender in the known F₁ hybrids, and none of the hybrids found in nature have yellow flowers. An independent origin for this color trait is not improbable as evidenced by *I. hartwegii*, which is closely related to *I. tenax* and has yellow flowers and by the fact that there are yellow-flowered forms in *I. macrosiphon* which is otherwise purple-flowered.

HYBRIDS BETWEEN *I. DOUGLASIANA* AND *I. INNOMINATA*

Iris douglasiana is a tall species averaging about 60 centimeters in height and is characterized by leaves about a centimeter wide; a branching stem; lanceolate, opposite bracts; large pale purple to white flowers; and a perianth tube 1 to 2 centimeters in length. Two or three flowers per branch are produced. Distribution of the species in Oregon is limited chiefly to a narrow, open coastal strip from Coquille, Coos County, southward. The species normally extends inland only along river valleys. It has not been seen in dense shade.

Iris innominata is a low species averaging about 35 centimeters in height and is characterized by narrow leaves which are about 4 centimeters wide; simple stems; ovate, opposite bracts; small, golden yellow flowers; and a perianth tube 1 to 2.5 centimeters in length. Distribution of the species is limited to the open meadows and hills of southern Douglas, Coos, and Curry counties, Oregon.

Hybrid colonies of about 100 plants each of the *I. douglasiana* × *I. innominata* cross have been found along Saunder's Creek, Curry County, Oregon. The two sites are 1½ and 2½ miles from the Rogue River, 3 miles upriver from Gold Beach on the south side of the Rogue River. The colonies are found in cut-over forest land with most of the plants completely exposed to the sun, though a few are found in the shade of *Umbellularia californica*. Some of the individuals are similar to the known hybrids grown for cytological study. Perianth size and plant size appear to be intermediate between the parent species and the bracts are shorter and more ovoid than are those of *I. douglasiana* but are longer and narrower than those of *I. innominata*. These individuals may be F₁ hybrids. Other plants appear to be the result of backcrossing and segregation.

Aside from the demonstration of genetic continuity between species, the taxonomic significance of the hybrids is considerable. Some individuals from one of the hybrid colonies compare closely with individuals referred to *I. thompsonii* Foster. There is a strong suggestion of the hybrid origin of that taxon. *Iris thompsonii* has been collected along the Rogue River and along United States Highway 101 from Carpenterville to Brookings, Curry County, Oregon. In California, it has been collected along the Smith River, northeast of Crescent City, Del Norte County. The

species can be distinguished from *I. innominata* by the more lanceolate bracts and by the pale purple to lavender flower color. It also seems to be taller, averaging about 45 centimeters. These are characteristics which could be fixed by backcrossing of the *I. douglasiana* \times *I. innominata* hybrids to *I. innominata*.

A similar hypothesis can be erected to explain those specimens with more ovate bracts and lavender-grey flowers referred by Foster (1937) to a new variety, *I. douglasiana* var. *oregonensis*. Backcrossing of the intermediates of the *I. douglasiana* \times *I. innominata* cross to *I. douglasiana* could result in the fixing of these *I. innominata* traits in otherwise typical *I. douglasiana*.

While both assumptions are largely hypothetical, they are lent support by the occurrence of these variants in an area where the two species come together and hybridize. The only barriers seem to be ecological, though exact factors cannot be stated. The removal of the forest trees with the accompanying reduction in shade has apparently removed the barrier to hybridization in the case discussed here, but elevation and soil factors may be important in other locations. However, hybrids probably will be found wherever the hills of Coos and Curry counties are near the ocean and conditions are disturbed or where *I. douglasiana* extends inland along river valleys. In these areas, at least, the two species can be expected to occur together.

HYBRIDS BETWEEN *I. BRACTEATA* AND *I. THOMPSONII*

Iris bracteata is a tall species averaging about 50 centimeters in height and with a thick perianth tube 0.5 to 1.0 centimeter in length, a pedicel 3 to 6 centimeters long, and golden yellow flowers. Typically the leaves are a glossy green on the upper surface and glaucous on the lower. The species has been seen only in southwestern Josephine County, Oregon, and northeastern Del Norte County, California. Ecologically it is restricted to shaded places. The species is found in greatest abundance within ponderosa pine communities, but it is sometimes found on cut-over forest land under a cover of bracken fern.

Iris thompsonii has been discussed as a possible hybrid segregate of the *I. douglasiana* \times *I. innominata* cross. Colonies are best developed along the lower Smith River, from 12 to 15 miles northeast of Crescent City, California. In this location, the colonies are well established on open rocky hillsides, and have not been seen in the shade.

Proceeding northeastward from Jedediah Smith State Park in Del Norte County, over the Siskiyou Mountains into Oregon, the colonies become more shade tolerant. Color changes gradually from predominantly pale purple flowers to predominantly yellow flowers, though a few white-flowered plants are present. Bract characteristics appear to be intermediate between the two species, changing gradually from ovoid and 5 centimeters long, to narrower and 7 centimeters long. Height of the plant also becomes progressively greater as colonies nearer typical *I. bracteata* are

examined. Three miles north of the summit of the Siskiyou Mountains only typical *I. bracteata* has been seen.

No individuals similar to the known F_1 hybrids have been found in nature. The transition between the two species is gradual, probably because of ecological requirements which permit more hybridization and survival of most of the hybrid offspring.

HYBRIDS BETWEEN *I. BRACTEATA* AND *I. CHRYSOPHYLLA*

Distinct hybrids between these two species have not yet been clearly demonstrated. Despite the pronounced morphological differences between the two, only one individual has been secured which can be considered intermediate. The relationship of the perianth tube to the pedicel is reversed in these two species. *Iris chrysophylla* has a perianth tube 5 to 6 times longer than the pedicel. In *I. bracteata* the pedicel is 5 to 6 times longer than the perianth tube. In the intermediate specimen cited above, the pedicel is twice the length of the perianth tube, clearly not characteristic of either *I. chrysophylla* or *I. bracteata*. This specimen was collected near Bridgeview, Josephine County, Oregon, where the two species occupy the same general area.

Complementing this admittedly limited evidence, field examination reveals hybrid characteristics which are not readily demonstrable with pressed specimens. Near Cave Junction, Josephine County, there are individuals of *I. bracteata* with narrow perianth segments characteristic of *I. chrysophylla*. The hybrid origin of these individuals is supported by the fact that all the known hybrids involving *I. chrysophylla* as a parent exhibit the narrow perianth of that species. There are also individuals, in the Cave Junction area, of *I. chrysophylla* with perianth color similar to the golden yellow of *I. bracteata*. The known *I. bracteata* \times *I. chrysophylla* hybrid has golden-yellow flowers and all other crosses involving golden-yellow and pale yellow-flowered parents show the flower color of the golden-yellow parent.

TAXONOMY. Due to the absence of cytological barriers between taxa and the presence of natural hybrids, nomenclatural revision which will better reflect the biology of the organisms seems necessary. Therefore, the following new combinations are proposed. Further field work is needed before accurate limits can be set for the California members of the subsection and they will not be considered here.

1. **IRIS TENAX** Dougl. subsp. **TENAX** (*I. tenax* Douglas ex Lindley, Bot. Reg. xv. t. 1218, 1829). This subspecies includes the typical form which has been discussed previously in this paper as *I. tenax*. Also included, without nomenclatural distinction, is the yellow-flowered *I. tenax* var. *gormanii*. The yellow-flowered form from Monument Peak, Linn County, Oregon, will be included within *I. tenax gormanii* and therefore within *I. tenax tenax* without nomenclatural distinction.

2. **IRIS TENAX** subsp. **CHRYSOPHYLLA** (Howell) (*I. chrysophylla* Howell, Fl. N. W. America 1:633, 1902). No type specimen was designated

for Howell's *I. chrysophylla*. However, filed with the type specimen collection at the herbarium of the University of Oregon is a specimen labeled "Type specimen" in the distinctive handwriting of Thomas Howell. This specimen, collected at Grants Pass, Josephine County, Oregon, in May 1887, must be considered the type specimen for Howell's species and therefore for the proposed subspecies.

3. IRIS TENAX subsp. BRACTEATA (Watson) (*I. bracteata* Watson, Proc. Amer. Acad. 20:375, 1885). This subspecies includes the species as described by Watson.

4. IRIS TENAX subsp. DOUGLASIANA (Herbert) (*I. douglasiana* Herbert, Bot. Beechey Voy. 395, 1841). Included in *I. tenax douglasiana* without nomenclatural distinction is *I. douglasiana* var. *oregonensis* Foster. So long as it is understood that Foster's variety is probably of hybrid origin, there is no need to distinguish a form which obviously belongs to what has been described as *I. douglasiana*. Since this subspecies is found in California as well as Oregon, this new combination must necessarily include the California plants. This does not mean that the California plants of this taxon should be ignored in any further study. There is undoubtedly considerable variation present that is not included in the Oregon representatives.

5. IRIS TENAX subsp. INNOMINATA (Henderson) (*I. innominata* Henderson, Rhodora 32:23, 1930). This subspecies has been retained as originally described except for the reduction in rank.

6. IRIS TENAX subsp. THOMPSONII (Foster) (*I. thompsonii* Foster, Rhodora 38:199, 1936). The only real difference between this proposed new subspecies and *I. tenax innominata* is in the purple flower color of *I. tenax thompsonii*. Since it has been suggested that *I. tenax thompsonii* may be of hybrid origin with *I. tenax innominata* as one parent, a close morphological relationship is to be expected. The two taxa differ slightly in distribution, *I. tenax thompsonii* is a species of elevations between 400 and 1000 feet while *I. tenax innominata* is usually at sites over 1500 feet. For that reason and because *I. tenax thompsonii* does form distinct colonies, it is retained.

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